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FACTORS INFLUENCING WHITE SPRUCE REPRODUCTION IN MANITOBA AND SASKATCHEWAN

GENERAL SCIENCES

ONE WEEK LOAN

by

J. S. ROWE

Forest Research Division
Technical Note No. 3
1955

Published under the authority of the
Minister of Northern Affairs and National Resources
Ottawa, 1955

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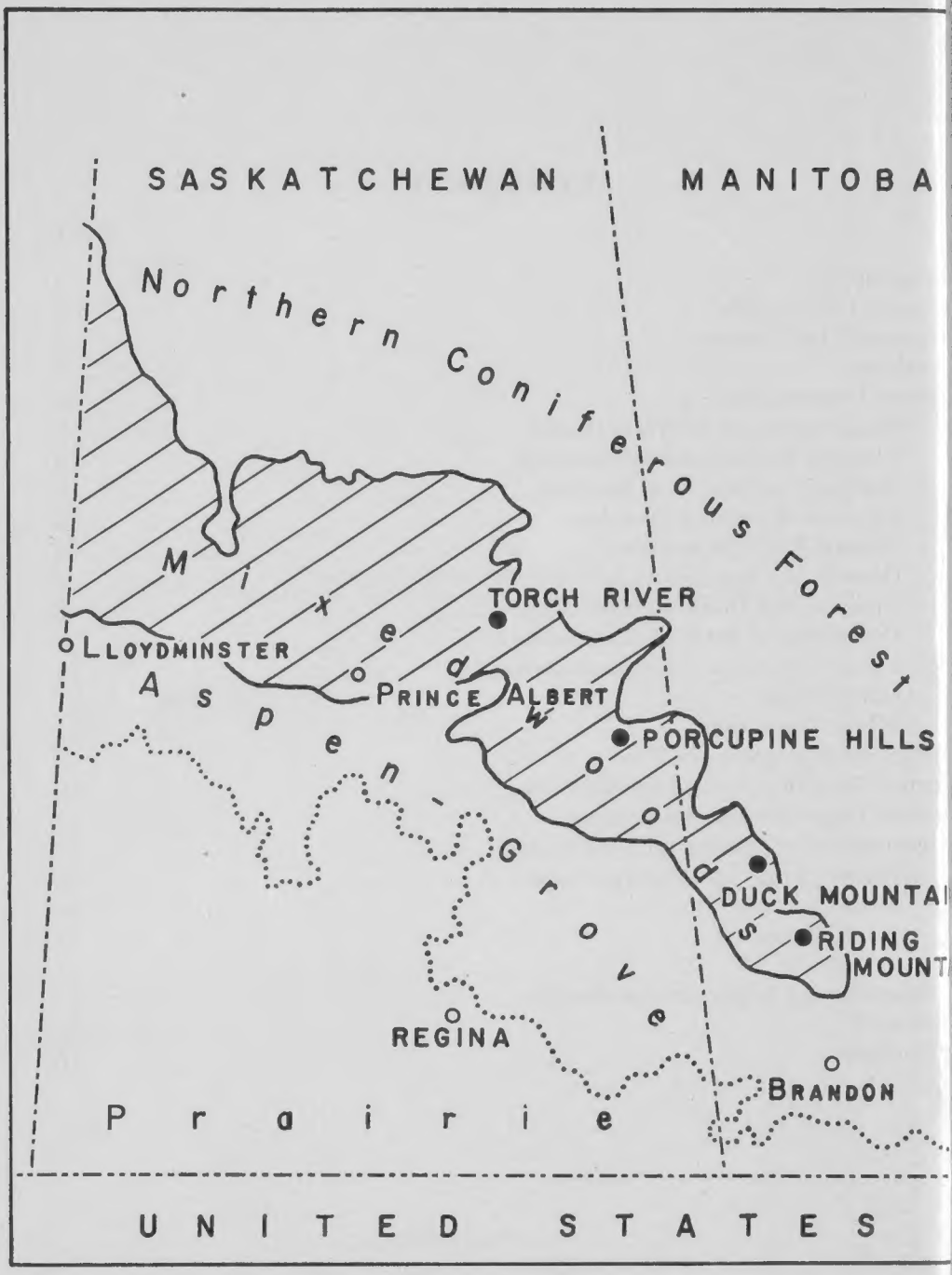

Figure 1. Location of Study Areas. (Shown by black dots).

Factors Influencing White Spruce Reproduction in Manitoba and Saskatchewan

PROJECT M. S. 135

by

J. S. Rowe[1]

INTRODUCTION

A study of the problems of spruce reproduction in Manitoba and Saskatchewan was begun in 1947 as part of the Federal Forestry Branch's general investigation of reproduction on cut-over and burned-over areas east of the Rocky Mountains. Preliminary surveys indicated that white spruce (*Picea glauca*[2]), locally the most important economic species, was regenerating poorly on logged or burned areas (Candy, 1951). Earlier research in this district had pointed to the same conclusion (Phelps, 1940).

During the summers of 1949 to 1951, field studies of a broad ecological nature were carried out on areas examined during the initial phase of the work, in order to gain a better understanding of the reasons for success or failure of reproduction. This report, which was submitted for publication in April, 1952, is concerned with the findings of these studies.

LOCALE OF THE STUDIES

The B.18 Mixedwood Section of the Boreal Forest Region as defined by Halliday (1937) is roughly triangular in outline, with its base in northwestern Alberta, and the apex in southwestern Manitoba. The studies were made in the eastern extension of this forest Section in Manitoba and Saskatchewan; in the forest stands on the uplands of the Cretaceous escarpment (Riding Mountain, and Duck Mountain, Forest Reserve); and in the stands of the lower adjacent lands to the north and west (the western Porcupine and Torch River Forest Reserves). (See Figure 1.)

Topography and soils are quite variable within the Section. On the uplands (above approximately 1,500 feet) topography is undulating to rolling, and surface deposits are formed of morainic materials varying in texture from sandy loams to clays, stone-free to very stony. The influence of post-glacial lakes on the lower lands has been extensive, hence the topography is not extreme, though the textural range of surface deposits is wide. Soil profile development is variable from place to place as would be expected. The majority of the profiles examined on well-drained sites appeared to be variants of the grey-wooded podzolic type, characterized by the presence of a grey, or brownish-grey, leached, platy A_2 horizon, a brown nutty B, and a lime accumulation at from 1 1/2 to 3 feet depth marking the top of the C horizon.

White spruce and aspen *(Populus tremuloides)* are two principal tree species; growing generally in mixture, they give the name "mixedwood" to the forest.

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[2] Nomenclature follows Gray's *Manual of Botany*, ed. by M. L. Fernald, eighth edition. American Book Co., N.Y., 1950.

Of less importance are black spruce *(Picea mariana)*, balsam fir *(Abies balsamea)*, balsam poplar *(Populus balsamifera)*, and white birch *(Betula papyrifera* Marsh.). Jack pine *(Pinus banksiana)* is locally important on drier soils, while tamarack *(Larix laricina)* and black spruce often form pure stands on wet sites.

Because topography is important in controlling soil moisture, forest types show a marked relationship to it. Though fires and logging distort the pattern, the tendency can be seen for spruce to establish itself in greater abundance on the moister sites, that is, on lower rather than on upper slopes, with aspen showing the opposite tendency. Hence the following types are commonly encountered: "Swamp Spruce" or "Spruce Flat" type, "Aspen Ridge" type, and the "Mixedwood Slope" type. Each presents a somewhat different problem with regard to spruce reproduction.

HISTORY OF THE LOCALITY

It seems likely that fire has played an integral part in the ecology of the Boreal Forest in the past. Charcoal can always be found in the humus layers of stands, with the exception of those which represent recent forest invasions of grassland. Furthermore, there are very few old forests to be found except in wet places or where topographic features afford protection from fire. Records of the ages of poplar stands and of fire scars on old spruce indicate that fires were prevalent in this region around the years 1822, 1853–55, 1889–91, and 1918–19. Recent bad fire years were 1937 and 1942.

Logging has been carried on for a long time though heavy cuttings were not made until the beginning of the century. At present most of the accessible spruce has been cut, and logging of the last remaining old growth is proceeding rapidly. The best stands have yielded from about 10,000 board feet of spruce per acre in the Riding Mountain Reserve to 25,000 board feet per acre in the Torch River Reserve.

METHODS

After preliminary reconnaissance of each new district, areas were selected for study which in species composition, stage of development of vegetation, topographic position, or other features, appeared likely to shed light on the problem of white spruce reproduction. Wherever possible, cut-over and burned-over areas were compared with residual or undisturbed forests. The unit of detailed study was a plot, square or rectangular, usually one-tenth or one-fifth acre in size. On each plot notes were made on the total plant community and on as many of the habitat factors as equipment and time allowed. Ages of the stands were established from the plots as accurately as possible by increment borings. Trees were tallied by diameter classes and heights of dominants measured. Minor vegetation was tallied by frequency and cover-abundance on 20-milacre quadrats mechanically spaced over the plot. Spruce seedlings and saplings were closely examined as to their rooting habits, ages, heights and rates of growth, and their positions relative to differences in microtopography. Generally, a soil pit was dug near the centre of the plot and a complete profile description recorded. Other factors such as biotic influences were noted as field conditions suggested.

During the summer of 1951, much of the time was spent in a detailed study of reproduction on ten 10-acre compartments of mature spruce-aspen at the Research Area, Riding Mountain National Park. Particular attention was given to the survival of spruce seedlings which had become established on strips ploughed in 1947.

SPRUCE REPRODUCTION

It is difficult to generalize about the reproduction of white spruce. Not only is the process complex at any one place, but it varies according to location. Each area has a unique combination of historical circumstances and site factors reflected in its particular plant (and animal) community, whose development therefore differs to some extent from that of every other community. As a constituent species, spruce is affected favourably or unfavourably in its establishment and survival by the special features of each community as well as by those features common to all.

Some of the general conditions of reproduction will be discussed first. In subsequent sections reproduction will be considered in relation to succession and to specific types of disturbance.

Seed Production of White Spruce

In mixed stands of spruce and aspen all evidence from these studies points to the beginning of seed production when the spruce are 45 to 60 years old.

Mature trees do not produce seed every year. On the Riding Mountain Research Area there were three good seed years in the period 1940–50, namely, 1942, 1944, and 1948. Following the latter year, in which the crop was very heavy, there was a complete failure and no cones were observed on any of the spruce. Records of cone production for the Duck Mountain and Porcupine Forest Reserves since 1911[1] indicate heavy crops for 12 years out of 40, or once every three or four years. The longest interval without a heavy crop was four years.

The seed ripens about the end of August and most of it is released during September. However, a small amount of seed has been found on occasion in cones which persisted on the trees into the following summer. This may provide the explanation for the scattered seedlings which sometimes appear after severe spring or summer fires have apparently destroyed all available seed by consuming the surface humus layer. On the other hand the seed may have been blown in from distant seed trees.

The greatest distance of seed dispersal which could be accurately determined in the field was five chains, or 330 feet. However, the seed is probably blown much farther than that. Assuming that the seed of white spruce falls at the same rate as that of red spruce, namely, 4 feet per second (Siggins, 1933), then the maximum theoretical range of dispersal from the top of an 80-foot tree in a 40 m.p.h. wind would be 1,176 feet. Turbulence and convection currents might greatly increase this distance. It is likely too that late falling seed is sometimes skidded by the wind for a considerable distance over a snow crust.

The seed may lie over at least one year on the ground before germinating, though almost all of it germinates during the first summer. Field observations in 1949 and 1950 showed the peak of spruce germination to be in July, and in 1951, weekly examinations of 200 small plots under a mature mixed stand on the Riding Mountain experimental area showed that germination began in the third week of June and reached its maximum during the first two weeks of July.

[1] Courtesy of C. B. Gill, Manitoba Forest Service.

Climatic Factors and Germination

Spruce germinates were found under practically all conditions of shade and exposure, provided always that the substratum was moist. Of particular interest was the appearance of great numbers of seedlings under the closed canopies of dense spruce stands. This condition was observed on bare needle litter and again where the forest floor had only a light covering of mosses and purple oat grass (*Schizachne purpurascens*). Though it would seem that moisture is all-important, low temperatures undoubtedly prevent germination early or late in the growing season, even though the surface layer is moist. In 1951, appreciable germination did not occur until the warm weather of early July, though records of precipitation and humidity showed exceptionally favourable moisture conditions throughout June. However, the problem of reproduction is not so much one of germination as of survival.

Surface Conditions and Survival

In considering early survival of the seedling one important fact should be kept in mind: every white spruce tree must grow from a small seed. Like all seed-dependent plants, spruce is at an initial disadvantage with species which can reproduce vegetatively such as the hardwood trees, the shrubs, and, with few exceptions, the forest herbs. It is well known that annuals, the seed-dependent plants *par excellence*, thrive where perennial competitors are sparse, as on recently disturbed areas. Significantly, lists of plants from many stands show that there are very few annuals represented in the flora of the undisturbed forest, and those that do occur make up an insignificant part of the vegetation. Examples are: *Circaea alpina* and *Impatiens capensis* in locally wet places; *Corydalis sempervirens, Corydalis aurea, Gentiana amarella,* and *Halenia deflexa* on thin humus, generally in open woods. It is not surprising then that spruce has trouble in establishing itself in normal undisturbed stands.

The first-year seedling develops a stem only about one inch tall surmounted by six cotyledons, and below ground a thin sparsely-branched root about two inches long. Such a small plant has difficulty in competing, both above ground for light and below ground for moisture, with the numerous neighbouring perennial species which every year send up large vigorous shoots from their well-established roots. In addition to the summer hazards of shading and drought, the seedling is exposed to the danger of mechanical smothering by the annual leaf accumulation from herbs, shrubs, and hardwood trees in the autumn. Field observations indicate that this may be the most important cause of mortality in the first few years. Thus spruce has its best possibilities of survival where conditions prevail which tend to prevent other plants from closing in and monopolizing moisture, light, and space. Such conditions generally exist on decayed wood and on disturbed (i.e. scraped or severely burned) mineral soil.

Decayed Wood as a Seed-bed

The presence of seedlings of certain conifers on rotting logs and stumps, especially in old forests, has often been commented on both in America and Europe. Jones (1945) stated that only a limited number of species have the ability to grow on this substratum: for North America he mentions species of *Picea, Tsuga,* and *Thuja,* as well as *Betula lutea.* To this list *Betula papyrifera* can be added on the basis of observations made in these studies.

Phelps (1940) in his survey of forest conditions in the Porcupine Hills estimated that 90 per cent of all spruce seedlings were rooted in decayed wood. Certainly this is the favoured surface medium in most stands, at least in the absence of any drastic disturbance of the humus layer. Though no attempt

Figure 2. White spruce seedlings (7 and 12 years old approximately) growing on a rotted stump, 40 years after logging. Reserve, Saskatchewan, 1949.

was made to determine the exact reasons for this phenomenon, it has been shown that decayed wood usually holds more available moisture than ordinary humus (Place, 1950), and therefore is the preferred substratum for spruce seedlings. White spruce wood seems to be more suitable as a seed-bed than poplar wood, as it is more retentive of moisture owing to bark and wood characteristics. Furthermore, there is no great drain by other plants on the moisture supply as only a relatively few species seem able to grow on rotted wood, species such as *Linnaea borealis*, *Trientalis borealis*, *Rubus pubescens*, *Cornus canadensis*, and *Circaea alpina*, plus, of course, many mosses. Position is undoubtedly important, and on logs and stumps, seedlings are well above the forest floor, safe from covering by broad leaves in the autumn. Other probable advantages of position are:

(a) Improved light conditions—stumps at least are generally beneath openings in the canopy;

(b) Improved temperature conditions—Mork (1933) claimed that logs and stumps showed higher temperatures than the germination layer of the adjacent soil;

(c) Freedom from damping-off fungi, and better mycorrhizal development, as suggested by Baldwin (1927). The mycorrhizal condition was found to be prominent on all seedlings that grew on decayed wood.

A comparison of the ages of seedlings on cut logs and stumps with time since cutting, indicated that between 20 and 30 years are required in normally moist mixed stands for "down" wood to decay to the point when spruce can successfully seed in.

Mineral Soil as a Seed-bed

Disturbances which expose mineral soil not only assist regeneration by providing a suitable seed-bed but at the same time eliminate competing plants. Thus, severe fires, by burning off the humus layer, destroy most of the species rooted in it. Similarly, surface conditions favourable to spruce seedlings are sometimes provided where the trampling of animals along game trails has exposed mineral soil, or where the wind has uprooted spruce trees. Violent wind storms which uproot spruce usually break off poplar trunks some 10 or 20 feet above the ground—consequently wind damage in a hardwood stand does little to encourage the invasion of spruce. Whenever soil is exposed, various species with mobile seeds appear, such as dandelion, sow thistle, and asters, as well as spruce.

Figure 3. Vigorous 7-year-old white spruce seedlings at the base of a fallen tree on mineral soil. Reserve, Saskatchewan, 1949.

Growth and Survival

The longer a spruce seedling remains small the longer it is exposed to the dangers that beset all small plants, for example, smothering by leaf fall, grazing by rodents, or shading by taller plants. Rate of growth therefore, plays a decisive role in survival. Of the two seed-beds most favourable for germination and early survival—decayed wood and mineral soil—the latter encourages much the better rate of growth. (See Table 1.)

Measurements of older seedlings and saplings indicated that spruce on mineral soil reach breast height at about 10 to 15 years of age but that those rooted in decayed wood in the forest require 20, 30, or more years. Thus the development of young trees on rotted wood under undisturbed stands is slow and precarious, compared to what it may be after drastic disturbance which destroys the canopy and exposes mineral soil.

TABLE 1.—COMPARISON OF SEVEN-YEAR SEEDLINGS ON DECAYED WOOD AND ON MINERAL SOIL

Porcupine Hills Forest Reserve

Site	Average height of the 50 tallest seedlings found
Severely burned area—moist ashy mineral soil under light cover of poplar	24·2 inches
Logs and stumps—moist decayed wood under moderate cover of spruce-poplar, and poplar	5·7 inches

Development of the roots, as of the tops, is apparently stronger on mineral soil than on decayed wood. Seedlings examined in 1949 on a very moist burned area, lightly shaded by young aspen, had extensively developed lateral roots. One seven-year seedling had roots extending three feet out from the base of the stem, though the tap-root penetrated only about six inches. On drier sites there was a greater development downward: a typical seven-year-old seedling for example sent its tap-root more than 24 inches down, but its laterals spread only some 16 inches to the sides. In marked contrast, the young spruce growing on decayed wood in shaded forest stands showed a weak development of the root system. Roots tended to grow parallel to the axis of the old trees, i.e. vertically in upright stumps and horizontally in logs on the ground, following the lines of decay. There was little sign of seedling roots leaving the decayed wood for the soil beneath.

Older spruce develop extensive shallow lateral roots from which vertical "sinkers" descend into the lower soil. Such a root system gives spruce the advantage over the deeper-rooted hardwoods in competition for moisture descending from the surface. There were instances seen where 60- to 80-year-old spruce had practically eliminated birch and poplar from what had been mixed stands, apparently through root competition, as the hardwoods had not been overtopped.

Climatic and Biotic Influences

The Mixedwood forest lies at the northern edge of the Grassland Formation, separated from it by the Aspen Grove transition zone. Its position indicates that moisture conditions for tree growth are barely adequate; relict prairies on drier sites within the forest show just how close to critical the moisture factor may become. It is not surprising then to find that, other things being equal, regeneration and growth of white spruce are favoured on seed-beds which hold precipitation (e.g. decayed wood) or which receive run-in water (e.g. the humus on lower slopes).

White spruce seedlings break dormancy about the first of June. Heavy frosts often occur after this date, particularly in low-lying areas, and in 1949 and 1951 many newly flushed needles of seedlings had been frost killed in grassy openings, wet depressions, and along edges of streams. Regrowth of the frost-damaged plants in the same year was rare; in all probability several successive seasons of late frosts would be sufficient to kill them. The needles of black spruce flush five to ten days later than those of white spruce, giving the former species a survival advantage on low ground.

The influence of various rodents on spruce reproduction was observed in some places. Hares sometimes feed on the buds and smaller twigs during the winter. On open burns, little or no damage of this type was found, most of it

being confined to aspen-covered or brushy areas. There were examples of spruce up to three feet tall which apparently had been killed by repeated cutting back of the terminal shoots and side branches. Examination of 25 seedlings in one area showed that most had been grazed in the period 1942–44. This corresponds to the high for the rabbit cycle which was reached in Western Canada in 1942, and in the Lake States a year or two later (Aldous and Aldous, 1944). The next period of maximum damage may be expected from 1952–54.

Voles were very abundant in the Riding Mountain area in 1949 (following the heavy seed crop of 1948) but they disappeared in the following season. They may have an important effect on the amount of overwintering seed, particularly when a maximum in their population cycle coincides with a medium, or poor, seed year. Observation suggests too that squirrels take most of the spruce cones and seed except in heavy seed years.

Periodicity of Seedling Establishment

The preceding sections have pointed out how reproduction on any site depends on seed production and distribution, seed-bed quality, and favourable climatic and biotic factors. These variables fluctuate more or less independently, but natural reproduction at any given time is related to their combined effects. In undisturbed forests the small amount of receptive surface is doubtless the limiting factor. Disturbance may increase the quantity of favourable seed-bed but climate, seed production or some other essential condition may then have a limiting effect. Only when a favourable coincidence of the fluctuating variables occurs is there likely to be establishment and survival on any large scale.

Measurements of the ages of several thousand white spruce seedlings during the summers of 1949 and 1950 provided evidence of periodic establishment. The data were collected over a wide range of sites and conditions—in burned, cut, or undisturbed stands, on decayed wood, mineral soil, or humus. Age of each seedling was determined by counting the number of bud scar rings (and associated whorls of branches) on the main axis. Table 2 shows the distribution of seedlings 10 years and younger by age-classes.

TABLE 2. -ABUNDANCE OF SPRUCE SEEDLINGS ON VARIOUS SITES BY AGE-CLASSES

Location and Areas Sampled	Ages in autumn, 1950										Total Seedlings Counted
	1	2	3	4	5	6	7	8	9	10	
Riding Mountain— Counts made on 4 Areas —cut-over, burned, and undisturbed	4	*78* (39%)	20	11	12	*23* (12%)	8	16	7	21	200
Duck Mountain— Counts made on 5 Areas —cut-over, and burned	5	*111* (17%)	21	30	69	*171* (26%)	56	85	45	57	650
Torch River— Counts made on 5 Areas —cut-over, and scarified	12	*151* (42%)	37	35	21	*68* (19%)	7	13	6	10	360
Porcupine Hills[1]— Counts made on 10 Areas —cut-over, and burned		Many[2]	4	28	80	*344* (23%)	315	*667* (44%)	40	37	1,515

[1] Ages advanced one year from 1949 data to make them comparable to data collected in 1950 on the other three forest reserves.

[2] Though one-year-old seedlings were extremely abundant in the Porcupine forests in 1949 they could not be considered as established, hence were not counted.

The broad similarity in the reproduction pattern regarding two-year and six-year seedlings is particularly interesting because it occurs over a 300-mile strip of the B.18 Mixedwood forest. A number of six-year seedlings may have been mistakenly tallied as seven-year-olds in the Porcupine data because, at the time of counting, it was not realized that favourably located seedlings sometimes grow from 1/4- to 1/2-inch beyond the cotyledons in the first year, resulting in two scars for a single year's growth: one at the cotyledons and one at the terminal bud. Only in the Porcupine Reserve were eight-year seedlings common, though some experimental plots on the Riding Mountain area which were burned over in 1940 seeded in naturally two years later, and in 1950 showed a vigorous population of eight-year spruce seedlings.

Further similarities in the four forest reserves were noted. For example, seedlings 12 to 25 years old were uncommon except in a few favoured spots, either through negligible reproduction during the 1930's (perhaps owing to the drought in those years), or because those that did become established have died out subsequently. On the other hand "thickets" of spruce and fir, 25 to 40 years old, were found frequently, especially under mature open mixedwood stands. Also, age frequencies of balsam fir seedlings growing in the same areas as the spruce showed a similar age pattern; the majority of those under 10 years of age were either two or six years old in 1950.

THE FOREST COMMUNITY AND REPRODUCTION

Cover Types

A natural successional sequence is represented by the three commonly defined cover types: the hardwood (coniferous component less than 25 per cent), the mixedwood (coniferous component 25 to 75 per cent), and the softwood (coniferous component more than 75 per cent). Spruce reproduction is intimately related to this sequence.

The pure poplar stands which spring up after fire or clear cutting are sooner or later invaded by spruce in the normal course of events. The succession from a hardwood to a mixedwood type is sometimes prevented because all seed sources have been destroyed; the hardwood type is then relatively permanent. However, spruce charcoal can usually be found in the humus layer, showing that the site formerly supported coniferous growth and may do so again when seed becomes available.

Invasion commonly waits upon the maturation of a few spruce which seeded in at about the same time as the poplar stand began growth. When these reach seed-bearing size, at age 60, or so, the progression toward a mixed type is initiated. The progress of invasion thenceforth is governed by quality and quantity of suitable seed-bed, by moisture conditions, and other factors of site rather than by seed.

The majority of the seedlings examined in poplar and in poplar-spruce types were rooted in decayed logs. Some were growing on moist humus in depressions. Not uncommonly, seedlings were found established on the raised hummocks at the bases of living aspen where presumably the lack of mechanical competition from leaf accumulation is a favourable factor. That seedlings survive in this position is shown by the "twinned" spruce and aspen which are common in some of the more advanced stands, obviously a result of seedlings growing up beside the poplar. In the final stage the aspen die and their decayed stubs are found protruding from between the spruce roots. This suggests that the seeding or underplanting of spruce close beside poplar stems might be a successful technique.

The mixedwoods which eventually develop from hardwood stands do not appear to represent a stable type either. Many of them clearly show evidence of succession toward a softwood type. In fact it may be stated generally that old stands are coniferous stands. From this it must be concluded that the Mixedwood Section of the Boreal Forest owes its characteristic physiognomy to frequent disturbance.

On the Riding Mountain Research Area a tally of 100 acres in the mixedwood type, with trees 100 to 120 years old, showed the spruce component to be uneven-aged and represented in all size classes, while poplar (chiefly aspen) was comparatively limited both in age and in size distribution. The overmature aspen is dying at present without replacement, while the spruce continues to increase. Thus an uneven-aged softwood type is in the making.

An older stand on Singoosh Island in the Duck Mountain area may represent a further stage of development. This forest has not been burned for about 150 years. The last of the aspen died recently, leaving a somewhat open, coniferous stand. In soil and minor vegetation the site resembles that of the Riding Mountain area mixedwoods. Figure 4 shows a comparison of the two forest types.

Note the numbers of spruce saplings in the Riding Mountain stands, also the large population of aspen. On the other hand the scarcity of both hardwoods and of young spruce on Singoosh Island is what would be expected in an older forest. At some point in the progression from mixedwood to coniferous forest, when all favourable habitats are stocked, the establishment of spruce seedlings will be halted. At this stage balsam fir may successfully invade, especially on moist sites and stands 200 years or older are usually of the spruce-fir type.

The invasion of poplar by spruce, either rapidly or over a long period, and the subsequent dying of the poplar represents the typical development of coniferous stands on medium moist sites. Individual spruce trees appear to reach their largest size under the foregoing conditions of succession, since the density of the spruce is at first limited by the poplar. When the latter die out, the scattered spruce dominants are then free to grow virtually without competition from other trees.

Brief mention will be made of three other spruce types, which develop by different successional routes:

(*a*) *Swamp Spruce*

These white spruce stands represent an advanced stage in succession on wet sites. They may be formed where the spruce invades a wet grass meadow or willow swale, and often they occur as a zone around sloughs, between the tamarack and the upland spruce-poplar, much in the manner of black spruce. The site is too wet for aspen—though sometimes a few balsam poplar are present—and no other tree stage precedes the spruce. Since the wet ground allows good seedling survival, the developing stand is dense and individual trees are small. Basal area may be high however—up to 200 square feet per acre.

Typically the chief ground cover is of deep feather mosses, especially *Hylocomium proliferum* (L.) Lindb., *Calliergon Schreberi* Willd. and *Hypnum crista-castrensis* L. Shrubs are practically absent and herbs are not abundant, though *Equisetum arvense, Carex* species, and species of the *Orchidacae* are distinctive.

In some of the older stands there is evidence that balsam fir is invading and that the type may change to spruce-fir. If destroyed by fire these stands will usually regenerate themselves unless the water table rises, when succession may be thrown back to the meadow stage.

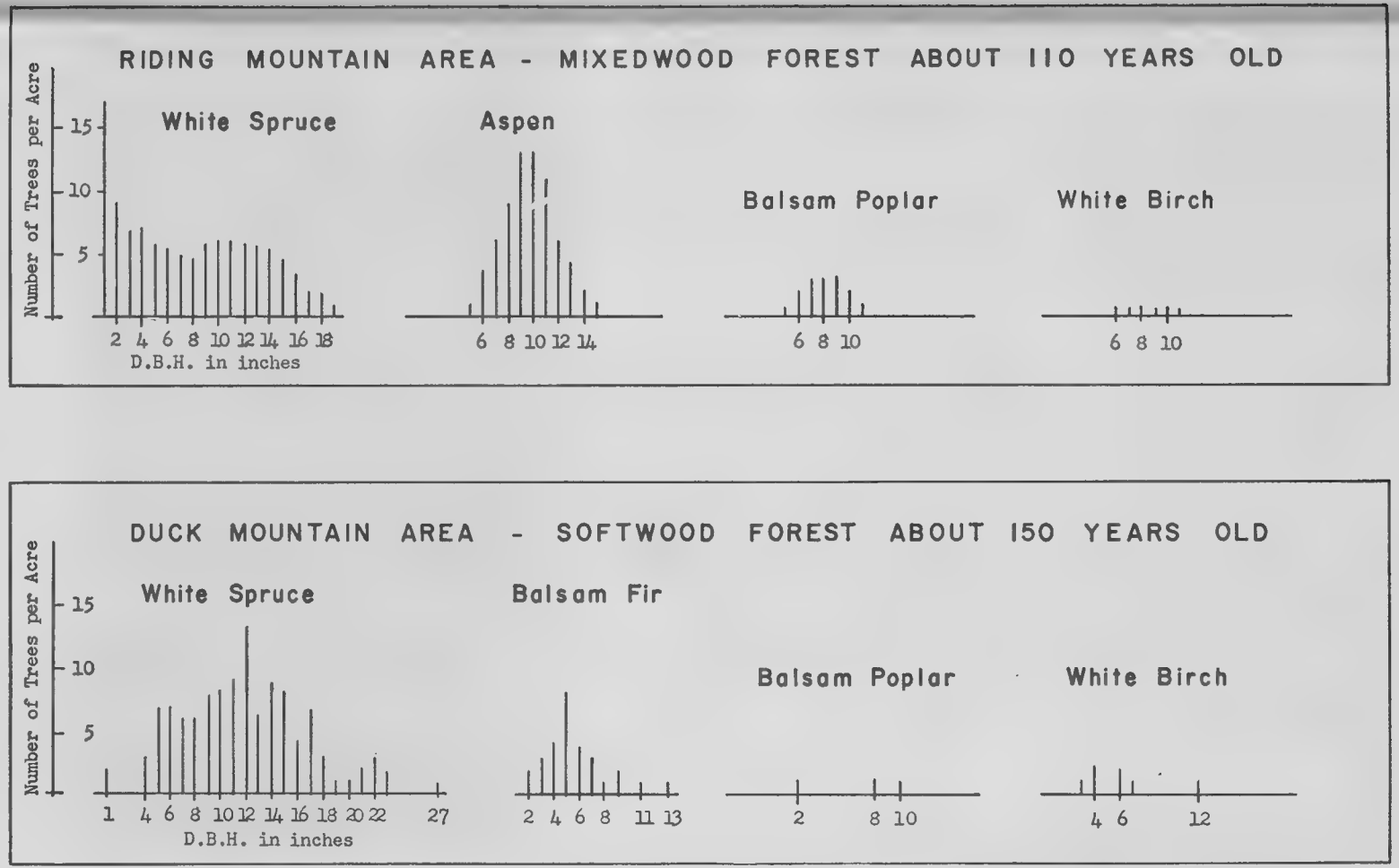

Figure 4. Comparison of two forest stands of similar origin and history showing number of trees per acre by diameter classes for each tree species.

(b) *Prairie Spruce*

"Prairie Spruce" stands represent the other extreme—a stage in succession on dry upland sites. Just as white spruce invades swamps without the intervention of an aspen stage, so it sometimes invades prairie communities, and thus appears to be more tolerant of habitat extremes than is aspen. Possibly the invasion takes place in particularly moist summers, for normally the soils of the prairies are dry, sandy, or gravelly. The actual invasion by young spruce can be seen at present in many places on the Riding and Duck Mountains; older stands are dense and individual trees are small. The type can readily be recognized by the minor vegetation which usually exhibits prairie species (*Antennaria Arabis*, etc.) plus *Schizachne purpurascens, Linnaea borealis, Pyrola* spp. and scattered feather mosses. Shrubs are sparsely represented, usually by *Rosa acicularis* and *Amelanchier alnifolia.*

(c) *Upland Fire Type of Spruce*

On uplands, dense stands of even-aged spruce are sometimes found which are obviously not the end result of either succession from meadow or from prairie. Generally they contain an admixture of poplar or birch, though these species tend to be crowded out before maturity. It was found that such stands invariably owed their origin to fires which had cleared the ground and made conditions suitable for immediate and complete establishment of spruce. Minor vegetation in these dense stands was very sparse, generally consisting of scattered tufts and patches of mosses (species of *Dicranum, Calliergon, Hylocomium*) plus *Cornus canadensis, Linnaea borealis, Petasites palmatus*, and others. (See pages 16, 17.)

Minor Vegetation

Spruce reproduction has been found associated with specific plant communities which either indicate a favourable habitat or themselves provide it. For example, it is not uncommon to find young spruce in the blue-joint (*Calamagrostis canadensis*) community on poorly drained flats, or growing under alder

Figure 5. "Swamp Spruce" type. The spruce has invaded a wet meadow. Reserve, Saskatchewan, 1949

(*Alnus rugosa*) and willows (*Salix* spp.) in moist draws and along streams. In these communities moisture is plentiful, the overstory is open, and broad-leaved herbs are not abundant. On the other hand, spruce seedlings are often found with such dry-site indicators as bearberry (*Arctostaphylos uva-ursi*), mountain rice-grass (*Oryzopsis asperifolia*) and northern rye (*Elymus innovatus* Beal) in open forests where minor vegetation is comparatively sparse and the humus is thin, or under hazel (*Corylus cornuta*) on well-drained uplands where presumably protection against leaf smothering is provided by the shrub's stems.

The plant communities mentioned above are representative of poorer sites, both wet and dry. Better sites—the normally moist—rarely regenerate to spruce unless decayed wood is present or the humus layer is disturbed. The chief unfavourable factor appears to be severe competition, mechanical and nutritional, from the dense growth of broad-leaved herbs such as aralia (*Aralia nudicaulis*), lungwort (*Mertensia paniculata*), and dewberry (*Rubus pubescens*). Shirley (1945) has claimed that the competition of minor vegetation is far more a hindrance to the success of coniferous seedlings than the overstory trees, and this appears to be true in the Mixedwood Section, at least on good sites.

Sometimes reproduction occurs in patches or thickets with individuals older in the centre than at the edges. Possibly the effect of the first established seedlings on snow accumulation, or on the surrounding minor vegetation, assists others to invade. This suggests that patch or group planting as advocated by Anderson (1951) might be worth investigating.

SPRUCE REPRODUCTION AND FIRE

Fire has been one of the most important influences determining the composition and development of Boreal Forest stands; with few exceptions forested areas have been burned and reburned in the past, hence it is important that some consideration be given to the effects of fire on spruce and associated tree species.

The frequency of fires, their severity, and the season at which they occur, all have an effect on the nature of the subsequent forest. Thus, stands burned in the spring and summer may fail to regenerate because all spruce seed has been destroyed, while stands burned at the time of cone-ripening or soon thereafter may immediately reseed themselves. In the West, unfortunately, the worst fire period coincides with the seedless part of the season—a twenty-year record in Saskatchewan shows that 87 per cent of all fires occur between April and August.

Where seed trees escape burning, regeneration may or may not follow according as the effects of other interacting factors are favourable or unfavourable. The following examples from field notes are given to illustrate some of the possibilities:

1. Reserve Fire, 1918, Reserve, Saskatchewan.
   (Examined in the summer of 1949—plots 31, 32, and 33.)

   Pre-fire type: Cut-over mature mixedwoods, as shown by the many large spruce stumps found at time of examination.

   Kind of fire: Not an extremely severe fire, at least on these study plots. The humus layer was partly destroyed but scattered seed trees survived, usually because of their location by wet depressions.

   Post-fire vegetation: A vigorous growth of aspen suckers followed the fire. In 1949, growth of shrubs and herbs was luxuriant, particularly hazel, dewberry, and aralia.

   Regeneration: Near the remaining seed sources a very few spruce seedlings were found.

Figure 6. Mature upland white spruce-aspen type. No spruce seedlings in the dense *Aralia* ground cover. Riding Mountain National Park, 1951.

Figure 7. Mature lowland white spruce type. Ground cover is chiefly grass (*Calamagrostis canadensis*) and tall herbs. Riding Mountain National Park. 1951.

Interpretation: Evidently the humus was only inflammable on the surface, the lower layer being too moist to burn (normal condition in the spring). Hence the perennating parts of the poplar and minor species were not destroyed but rather stimulated to vigorous growth. In the resulting dense vegetation, spruce seedlings have been unable to survive.

2. North Bertwell fire, spring of 1942, Bertwell, Saskatchewan.
(Examined in the summer of 1949—plots 41 and 44.)

Pre-fire type: White spruce with scattered poplar, originating after fire about 110 to 120 years previously.

Kind of fire: A severe fire which burned a corridor through the old stand, destroying the humus layer and exposing mineral soil. Seed trees only at the edge of the burn.

Post-fire vegetation: There was only weak suckering of poplar; the minor vegetation was sparse, consisting mainly of scattered dandelion, sow thistle, aster, and vetch. It is interesting that all minor species with the exception of the vetch were invaders from outside the burn.

Regeneration: Abundant spruce seedlings were found rooted in the ashy mineral soil. On the drier sites the seedlings were small, but where the clay soil was moist they were large and vigorous. Invasion had taken place in the year following the fire. Best growth was under a light canopy of aspen.

Interpretation: The humus layer, largely composed of resinous needles, burned completely thus eliminating all competing plants— excepting the few whose perennial parts entered mineral soil—and leaving an ashy clay exposed. The coincidence of a good seed crop in the autumn of 1942 made possible immediate invasion and establishment long before competition could become a significant factor.

Another very similar fire burned west of Bertwell in 1937. Spruce seedlings were found in large numbers on the ashy mineral soil near seed sources. The interesting point was that age counts showed the main wave of invasion to have taken place six years after the fire, at the same time as on the 1942 burn discussed above.

3. North Timberton fire, 1937. Timberton, Manitoba.
(Examined in the summer of 1950—plot 119.)

Pre-fire type: Cut-over coniferous stand with patches of residual poplar.

Kind of fire: Severity of burn had varied according to the stand composition from place to place, i.e. by the spruce stumps it had been severe, baring mineral soil, but in the vicinity of poplar the humus had only been partly consumed.

Post-fire vegetation: On clean burns by spruce stumps there was an open cover of dandelion, sow thistle, aster, twinflower, and vetch. Near poplar snags where the fire had not burned so deeply there was a dense cover of minor species, including dewberry, rose, strawberry, mertensia, snowberry, among others. Aspen suckers were more abundant in the latter than in the former positions.

Regeneration: Spruce seedlings were abundant and vigorous on the severely burned patches beside spruce stumps where weedy herbs grew. Elsewhere in the dense minor vegetation they were absent or quite rare.

Interpretation: Here is an illustration on one area of the effects of different degrees of burning. Evidently, under some conditions, the deep needle litter under spruce burns more thoroughly than the broad-leaf litter of aspen, shrubs, and herbs. The complete burn provides a suitable seed-bed free of competition where spruce seedlings thrive.

The "Whirlpool" fire of 1915 on the Riding Mountain Research Area represents an older stage of a burn similar to the above. Spruce regeneration is present as "thickets" of individuals up to 30 feet tall, each thicket almost invariably centred on an old stump. Where regeneration is absent there are only poplar snags to be found, that is, the seedlings and saplings are present only where spruce grew before.

4. "Riel" fire, *circa* 1890, Bertwell, Saskatchewan.
(Examined in the summer of 1949—plots 48 and 51.)

Pre-fire type: Chiefly mature white spruce with lesser amounts of poplar.

Kind of fire: A severe fire which in most places burned away the humus and exposed a stony clay-loam soil.

Post-fire vegetation and regeneration: Minor vegetation was not particularly dense and consisted mainly of dryland grasses (particularly *Oryzopsis asperifolia*) and herbs, indicative of a rather droughty soil. The sixty-year-old poplar stand had a well-developed understory of spruce seedlings and saplings, at least near remaining seed sources. However, the young spruce were not growing on mineral soil, but had established themselves on the decayed trunks of the fire-killed trees some 25 years after the fire, beginning about 1915.

Interpretation: Apparently mineral soil was not in itself sufficient here to guarantee regeneration. Perhaps the soil was too dry. But when the fire-killed spruce decayed they provided a suitable seed-bed and invasion began. There is thus a gap of 25+ years in ages between the poplar and spruce components of the stand.

The effects of topographic position were illustrated elsewhere on the same burn. Lower slopes supported many seedlings while upper slopes had few. The chief reason seemed to be that on the lower slopes where moisture conditions were better there had been more spruce prior to the fire. Consequently there was more decayed wood after the burn, hence more seedlings moved in.

These examples illustrate conditions commonly found on many other burned areas: light surface fires on normally moist sites make conditions unfavourable for spruce establishment because they stimulate the growth of perennial plants, but severe fires make successful establishment possible by simultaneously baring mineral soil and eliminating the competition of both plants and animals. Severity of fires depends in part on the degree of inflammability of the humus layer. It was noticed that fires almost always consumed the entire humus layer over well-drained, light-textured soils, but this occurred less often over clays. Hence the even-aged "fire-spruce" stands sometimes encountered were usually on sandy soils.

Though intense fires may improve seed-bed conditions, directly by baring mineral soil or indirectly by providing decayed wood, they do not guarantee spruce reproduction, but only improve its likelihood where seed availability, adequate moisture, temperature, and other necessary conditions are fulfilled.

SPRUCE REPRODUCTION AND SCARIFICATION

The common occurrence of spruce seedlings along logging roads, game trails, ditch banks, and similar places—in fact almost everywhere that moist soil is exposed—has suggested that scarification of the forest floor may be a useful technique for the encouragement of regeneration. By preparing a suitable seed-bed and destroying, or at least weakening, the minor vegetation, ploughing up the humus layer accomplishes somewhat the same results as severe burning, and does not endanger the residual forest.

A study of the effects of discing under an open mature mixedwood stand was begun in 1947 on the Riding Mountain Research Area. This stand[1] averaged 99 square feet of basal area per acre of which 53 per cent was contributed by softwoods (chiefly white spruce) and 47 per cent by hardwoods (chiefly aspen). Crown closure as determined by "Moosehorn" readings averaged approximately 57 per cent.

Strips were ploughed with a tractor-drawn disc plough at one-chain intervals through 90 acres of the forest type. Nine hundred small plots, each 1/8,000

[1] Described on page 12.

acre in size, were staked out on the ploughed strips and an equal number of controls of the same size were marked on the adjacent undisturbed humus. The numbers of new seedlings found in each yearly count since 1948 are as follows:

	Year of Establishment			
	1948	1949	1950	1951
Seedlings on disturbed plots	750	9,317	13	37
Seedlings on undisturbed plots	200	3,760	8	20

These counts show a close correspondence with the seed crop ratings of the preceding years based on visual estimates of cone production: these were medium in 1947, heavy in 1948, and nil to light in 1949 and 1950. The germination was always greater on the ploughed than on the unploughed plots: in 1949, for example, increase of new seedlings was in the ratio of about 5 to 2.

The following is a brief summary of information gathered in the summer of 1951:

1. A count of the 1949 germinates showed that, after three years, mortality on ploughed strips was 80 per cent and on controls 90 per cent, reducing the relative numbers from 5 : 2 (in 1949) to 5 : 1 (in 1951). Thus survival, like germination, has been better on ploughed strips.

2. Mortality during the year was least during the growing season and greatest from September to May, a great deal of it being traced directly to smothering by poplar leaves. Of 1,100 dead or dying two-year-old seedlings examined on ploughed plots, 50 per cent had definitely been crushed down by leaves, 33 per cent had been broken, though not covered (apparently animals trampling in the furrows accounted for most of this damage), and the remainder had died or were dying from miscellaneous causes, mostly unknown, but presumed to be competition, frost-heaving, fungal attack, and similar causes. There was a smaller percentage of smothering on the controls, but even here competition appeared to be at least as important to survival as were all other factors combined.

3. On the ploughed strips most of the seedlings were rooted in mineral soil though many were surviving where the plough had merely scraped away part of the humus layer. On the average, more seedlings were found on thoroughly scarified than on partly scarified, plots.

4. Irrespective of moisture conditions there was better survival on the sloping sides than on the flat bottoms of the furrows—probably because leaves collected in the latter position.

5. When stocked plots were grouped in four moisture classes (dry, moist, very moist, and wet) on a basis of topographic position, soil profile, and minor vegetation, it was found that the average number of seedlings per plot increased regularly from three on the dry to five on the wet. None of the "dry" ever had more than five seedlings, but numbers to 25 occurred on certain of the moist and very moist plots. In fact, over the whole 90 acres, most of the spruce advance growth (saplings and large seedlings) were found in and at the edges of the very moist *Alnus* swales and *Carex* depressions.

6. The great majority of all plots fell on normally moist upland clay and clay loam soils where the chief minor species were *Calamagrostis canadensis, Corylus cornuta* and *Aralia nudicaulis.* Each "moist" plot was assigned to one of three groups according to which of the above species was dominant within a half-chain radius of it. Examination of the three groups showed that the ratio of stocked to unstocked plots was highest in the *Corylus* type.

7. After four growing seasons the ploughed strips had, on the average, a 50 per cent cover of minor species. Some parts of the furrows were completely overgrown and could be located only with difficulty. The chief invading species were grasses and such herbs as strawberry, dewberry, and aralia. Obviously much of the value of discing will be gone after about five years.

8. The rate of growth of seedlings has been very poor even though recent growing seasons have been moist. In the autumn of 1951, the 1949 germinates were only two or three inches tall. Apparently, light and temperature are the limiting factors. This was indicated near the forest camp by the weekly terminal growth of spruce saplings which in 1951 showed a close correlation with the weekly sum of temperatures.

9. Tallies of the area were taken on nine separate 10-acre compartments, making possible a comparison of regeneration by blocks. The compartments differed somewhat in the relative importance of spruce and aspen but no correlations could be found between tree species (size, abundance, relative numbers) and either seedling abundance or frequency. There was no particular localization of seedlings; stocked plots were scattered over each compartment in a random manner. Plots near seed trees were no oftener stocked than plots farther from seed trees. Numbers of seedlings on ploughed plots bore no particular relation to numbers on their controls; where the ploughed had many, for instance, the control might have few, and vice versa. The lack of any correlation with the larger environment points to the importance of the micro-habitat in the reproduction of spruce.

The experiment has demonstrated the values of discing to encourage establishment of spruce seedlings, though it has also shown that subsequent survival and growth are not particularly satisfactory. A reduced density in the overstory might help to improve the latter, which suggests that scarification may be most successful when done in conjunction with logging.

SPRUCE REPRODUCTION AND LOGGING

Logging rarely assists spruce reproduction; sometimes it makes conditions very unfavourable. Opening the canopy often results in a prolific growth of herbs and shrubs, thus increasing competition on the forest floor. The old trees which in an undisturbed forest would eventually fall, decay, and provide suitable seed-beds are removed. The ground is only scarified locally along haul trails, and in winter logging may be scarcely disturbed at all. Phelps (1946) studied the Carrot River winter logging project and concluded that conditions for regeneration had not been improved by cutting. Bedell (1948) pointed out that although the nature of the residual stand would influence such matters as seed supply and

shelter, the system of cutting did not in itself provide a complete answer to the problem of regeneration because it often failed to counteract the unfavourable influences of the humus seed-bed. Evidently more drastic disturbance of the forest floor is required to initiate regeneration than that which results from the mere felling and hauling away of trees.

Logged areas were sometimes encountered which at first sight appeared to have regenerated well; closer examination usually showed that the young spruce had been established before logging and that very few of the seedlings "came in" afterwards. Only two areas were found on which spruce had reproduced adequately following logging; in both, better than normal seed-bed conditions existed. The stands were on moist sites where the original type at time of cutting (35 to 45 years previously) had been white spruce with scattered poplar. On one of the areas, every old spruce stump had from six to 20 seedlings on it, ranging in age up to 15 years. Scattered seedlings, rooted in decayed logs, also occurred on the ground between stumps. Obviously the presence of much moist rotted wood was the significant feature of the site. The second area was similar in having seedlings on the decayed stumps but in addition there were large numbers on the moist mossy humus. Here a high water table and a very moist surface layer combined with a sparse cover of herbs and shrubs had made conditions favourable for spruce seedlings.

Figure 8. Cut-over mixed woods showing residual poplar and dense shrub-herb undergrowth. Spruce reproduction is generally poor on such sites. Reserve, Saskatchewan, 1949.

Normally, cut-over areas are taken over by such a luxuriant growth of *Rubus idaeus*, *Corylus cornuta*, or *Calamagrostis canadensis* that the invasion of spruce is inhibited for a long time.

REPRODUCTION OF ASSOCIATED TREE SPECIES

Poplar (Aspen and Balsam Poplar)

Close examination of the ground during studies of minor vegetation showed that poplar suckers, one to two feet high, are commonly present on the forest floor under mature mixedwoods. As there are rarely any poplar of sapling size in these stands, it is clear that the suckers do not develop further. If the spruce is logged off and the stand opened, then the small poplar can shoot up, and this probably explains why the ages of second generation poplar are sometimes found to be one to three years older than the time elapsed since cutting.

Light fires stimulate suckering of poplar but severe fires which burn away all the humus weaken the species. An example was seen where fires in 1937, 1942, and 1946 had eliminated the aspen entirely, resulting in a weed-grass vegetation on what had been a well-forested site.

Because aspen does not invade upland relict prairies or wet peaty lowland soils as readily as does white spruce, fairly pure coniferous types are generally found on these sites.

Old poplar stands appear to lose their ability to sucker, and as the trees die and fall the site is taken over by shrubs. It may be that fire is necessary to renew such stands.

Birch

Birch is a prolific seeder; the seedlings are quite tolerant and, like poplar suckers, are often found on the forest floor. Once established, birch can maintain itself by coppicing. It depends on seed for migration, for unlike poplar it cannot spread by root sprouts. Some of the habitats suitable for establishment of spruce—decayed logs, peaty humus, moist soils after clean burns, and so forth—are also suitable for birch, and for this reason spruce-birch mixtures are not uncommon. In very old coniferous forests poplar dies out, leaving birch as the sole hardwood species. If such forests are burned, birch is often the chief hardwood invader. The distribution of birch can generally be explained by taking into consideration both seed-bed conditions when the trees got started, and the degree of competition thereafter.

Black Spruce

Black spruce usually produces viable seed at an earlier age than white spruce. Furthermore the seed is held in the semi-serotinous cones. A 35-year-old burn was examined on which thicket regeneration of both spruces was present with aspen. Many of the black spruce bore clusters of old and new cones but white spruce had none. Seed was collected and found to germinate and grow well. In all likelihood, another fire would eliminate the white spruce but not necessarily the black. Possibly the so-called "upland black spruce" type is to be understood by its fire history rather than in terms of site factors per se.

Balsam Fir

Halliday (1943) has pointed out that a map of the abundance of fir throughout Canada shows a marked resemblance to a map of mean annual rainfall, that is, fir is most abundant where rainfall is greatest. In line with this, field observations in local areas of Manitoba and eastern Saskatchewan show that fir is more abundant on the moister than on the drier sites of the mixedwoods. For example, there is not as much fir in the Riding Mountain forests as there is in the moister

forests of the Torch River area. The species does not invade the drier types of spruce and spruce-poplar stands but it does invade (and grow in) the moist feather mosses under a dense spruce canopy—something that spruce seedlings are unable to do.

Fir is heavily browsed by deer and elk, at least on the Riding Mountain area, but spruce is not. Where there are concentrations of these animals the browsing may be severe enough to kill seedlings and saplings, changing to a spruce type what might have developed into a spruce-fir type.

DISCUSSION AND APPLICATION OF RESULTS

In plant communities where the great majority of all the species have the power of vegetative reproduction, the few species which depend entirely on seed for their continued survival are at a great disadvantage. Such is the position of white spruce—a plant which can only appear as the result of germination of a small seed and survival of a delicate seedling. Compensation for this disadvantage lies in the relatively long life of the tree, whose seed-producing ability over the years keeps it in the mixedwood communities. Given enough time, spruce will reproduce, for eventually larger or smaller areas will be made receptive to seed either by some widespread disturbance such as fire, or by the local development of favourable spots within the undisturbed community.

The results of this study suggest certain methods for assisting spruce regeneration or for speeding up the process. Scarification of the forest floor prior to logging is recommended. Ideally the ground would be scarified just before a good seed year, and the forest would be cut as soon as seedlings were well established. In practice it is not yet possible to predict seed years, therefore the safest system would be to scarifiy about four years before the cut to allow sufficient time for at least one good regenerative season. There would probably be no advantage in discing earlier than this, as after about five or six years the strips will be overgrown by minor vegetation.

Various types of ploughing machinery should be used in experimental work. It seems likely, on theoretical grounds, that an implement which would throw up a high ridge would be more effective than the Athens disc-plough. Such a ridge would remain free of leaf accumulation for a long period, and would not be reclaimed by minor vegetation as quickly as disced ground; the bank of a drainage ditch was seen which had provided just such an excellent condition for spruce regeneration over a period of at least 15 years. In open stands where drought and high temperatures may prove lethal, a soil ridge ploughed up in an east-west direction should assist regeneration by providing shelter and improved moisture conditions, particularly along its north side.

Fire as a silvicultural tool can only be employed when weather and fuel conditions are just right. It must destroy at least the upper part of the humus layer if it is to assist regeneration of spruce; otherwise, it merely stimulates minor vegetation to more vigorous growth and increases the competition factor. Studies of the use of fire should be made, particularly where decadent or diseased stands require rejuvenation.

On severely burned areas broadcast seeding of spruce should be tried. The chances of success after a fire could be gauged by means of a ground survey to determine the degree of disturbance of the forest floor. The probability of getting spruce regeneration by seeding should be good wherever the humus layer has been completely destroyed, provided the surface soil is not too dry.

Selective seeding in hardwood stands and on lightly burned areas would merit investigation. Spruce seedlings have been found to establish themselves and survive where local conditions offer better than average moisture and protection from leaf fall. This suggests that seed spotting might succeed on decayed logs, beside stumps, at the bases of poplar trunks, along the edges of alder swales, and similar locations.

These studies make it apparent that planting, like seeding, should be particularly successful on ground cleared by fires. Where a conversion to mixedwoods is desired, underplanting spruce in hardwood stands close to the trunks of established trees would appear to be worth trying.

The occurrence of "thicket" regeneration in some hardwood and mixedwood stands suggests that patch or group planting may be a more effective technique than the usual spaced single tree method.

SUMMARY

A study of white spruce reproduction was made during the summers of 1949, 1950, and 1951 in the eastern B.18 Mixedwood Forest Section, from the Torch River Forest Reserve in east-central Saskatchewan to the Riding Mountain National Park in southwestern Manitoba. Cut-over and burned-over areas, as well as undisturbed forest stands, were examined to clarify the relationship between reproduction and stand history, vegetational succession, forest floor conditions, and other site features. Temporary plots of one-tenth-acre or one-fifth-acre size were established in conditions judged suitable for the purposes of the study, and notes were made on the total plant community and on the environmental factors in each.

Seed is produced in abundance by mature white spruce about once every three or four years. Germination is, however, largely dependent on adequate moistness of the ground surface during June and July. Survival of the delicate seedling is threatened not only by extremes of habitat conditions, to which competition from other plants for light and moisture contributes, but also by the smothering effects of the annual accumulation of herb, shrub, and tree leaves, particularly under hardwood and mixedwood stands.

The most favourable seed-bed in undisturbed forests is decayed wood. This provides a moist substratum and, as a result of elevation above the surrounding forest floor, a certain amount of protection from leaf accumulation. In disturbed stands where the humus layer has been burned or scraped away, conditions are also suitable for the establishment of spruce, for competition is temporarily eliminated and mineral soil (generally moister than the humus layer) is exposed. Seedlings have a better rate of growth on disturbed soil than on rotted wood.

Reproduction depends on a large number of fluctuating factors—seed supply, seed-bed, climatic conditions, influence of animals and plants, and others. To get large-scale establishment and survival favourable phases of all these factors must occur at an appropriate time. Excellent seed years in 1944 and 1948 have resulted in the appearance, by 1950, of numerous six-year-old and two-year-old seedlings over a 300-mile belt of the Mixedwoods.

Poplar stands are gradually converted to mixedwoods by the invasion of spruce, in the normal course at least. In the absence of fire, mixed stands tend to develop into softwood stands as the relatively short-lived poplar dies out.

There are other successional routes by which white spruce types may develop as where a sudden and complete invasion is made by spruce into meadow, grassland, or severely burned areas, without the intervention of a poplar stage.

Spruce seedlings are often found growing on extreme sites—the wet or the dry—where the minor vegetation communities are not unfavourable to establishment and survival. Severe competition prevents establishment on the better growing sites.

In general, light surface fires produce unsatisfactory conditions for spruce establishment because they stimulate the growth of competing plants. Severe fires favour regeneration of seed-dependent plants such as spruce by weakening competing species and exposing mineral soil.

Scarification of the humus layer has nearly the same effect as severe burning, as it favours invasion of spruce by reducing plant competition and exposing the soil.

Logging rarely counteracts the conditions of the forest floor unfavourable to the reproduction of spruce. The humus is not disturbed to any extent (particularly in winter logging), and the trees are removed which would eventually produce a rotted wood seed-bed. Only very moist sites seem to regenerate adequately.

The reproduction and growth of tree species associated with white spruce have been discussed briefly. Poplar is becoming ever more important owing to its ability to sprout following stand disturbance. Birch—like spruce -depends on seed for migration, and as the conditions favourable for its appearance are much the same as for spruce its seedlings too are often found on decayed wood or wet humus. Black spruce retains seed in its semi-serotinous cones and this habit combined with its ability to produce seed at an earlier age than white spruce, gives it an advantage over the latter species in the restocking of burned areas. Balsam fir appears to be on the increase on moist sites in undisturbed and cut-over coniferous stands. Very shade tolerant, it is able to invade under a dense white spruce canopy.

Some of the possible applications of the results of the study to practical silviculture have been outlined in the previous section.

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